

A revision of *Empodiodes* Oldroyd, 1972 with the descriptions of two new species from South Africa (Diptera, Asilidae, Stenopogoninae)

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Abstract

The genus *Empodiodes* Oldroyd, 1972, a Southern African endemic, is revised. Six species are recognised, four previously described (*E. greatheadi* Oldroyd, 1972, *E. melanoscopaeus* Londt, 1992, *E. namibiensis* Londt, 2012, *E. whittingtoni* Londt, 1992) and two new species (*E. pusillipes* **sp. nov.**, *E. torridus* **sp. nov.**). A key for their separation is provided and their distributions mapped and discussed.

Keywords

Afrotropical, assassin flies, robber flies, taxonomy

Introduction

Empodiodes Oldroyd, 1972 has been the subject of relatively recent taxonomic research, and the history of work on the genus fully expounded (Londt 2012). The following is a brief summary of developments to date.

- Oldroyd (1972) – Described the genus with his new species, *E. greatheadi*, based on a single male specimen from the Eastern Cape Province of South Africa, as genotype.
- Oldroyd (1974) – Redescribed the genus in an Appendix, providing his original illustrations. While making comparisons with other Stenopogonine genera he declined to allocate the genus to this subfamily.
- Oldroyd (1980) – Catalogued the genus and species within his Dasypogoninae.
- Londt (1992) – Revised the genus, recognising it as belonging to the Stenopogoninae and adding two new species (*E. melanoscopaeus* and *E. whittingtoni*) from the Northern Cape Province of South Africa.
- Londt (1994a) – Included the genus in a key to Afrotropical Stenopogoninae.
- Londt (1999) – Included the genus in a revised and updated key to Afrotropical Stenopogoninae.
- Londt (2012) – Described a new species, *E. namibiensis*, from northern Namibia and provided a key to the then four known species.
- Londt and Dikow (2017) – Included *Empodiodes* in a key to Afrotropical asilid genera and summarised the little that was known about the genus.

There were, therefore, four described species of *Empodiodes* at the commencement of this study (*E. greatheadi* Oldroyd, 1972, *E. melanoscopaeus* Londt, 1992, *E. namibiensis* Londt, 2012, *E. whittingtoni* Londt, 1992). With the discovery of two additional species this interesting genus requires further attention.

Materials and methods

Terminology follows mainly that proposed by Cumming and Wood (2017) as well as that used by the author in more recent publications. Specimens are housed in the following institutions:

AMGS	Albany Natural Sciences Museum, Makhanda (= Grahamstown), South Africa
BMNH	The Natural History Museum, London, UK
BMSA	National Museum, Bloemfontein, South Africa
NMSA	KwaZulu-Natal Museum, Pietermaritzburg, South Africa
NMWN	National Museum, Windhoek, Namibia

Material listed for each species is arranged according to geographical coordinates within countries (alphabetically). Material previously listed in publications is relisted in order to provide as complete a record of localities, dates of collection and field notes as possible. When available, label data are cited as it appears on labels, lines of information being separated by a slash (/). Database numbers, when available, are also provided. While more recently collected material is frequently provided with detailed information relating to locality and habitat, it has been necessary to attempt to establish reasonably accurate geographic coordinates for older or relatively poorly

documented specimens in order to gain a better concept of distribution. Google Earth and the Internet have been used to accomplish this. Information considered relevant, but not appearing on labels, is provided in square brackets. Wings were removed and placed in alcohol between two glass microscope slides for photography. These were then mounted on cards and attached to the pins of the relevant specimens. Terminalia were excised, macerated in hot Potassium Hydroxide (KOH), drawn with the aid of a drawing tube before being stored in micro vials attached to the relevant specimen pins.

Results

Taxonomy

Empodiodes Oldroyd, 1972

Empodiodes Oldroyd, 1972: 635. Type species: *Empodiodes greatheadi* Oldroyd, 1972, by original designation.

Diagnosis. (based primarily on key characters used by Londt and Dikow (2017)):

Head: Antennal stylus without long setulae. Head distinctly wider than high in anterior view. Facial protuberance only slightly projecting ventrally. Frons only slightly divergent. Eye more or less oval in lateral view. Mystax separated from antennal sockets by a distinct gap. Tentorial pits small, slit-like, inconspicuous ventrally. Proboscis straight. Palpus 2-segmented.

Thorax: Prosternum separated from proepisternum by membranous area. Anepisternum lacking strong macroseta at superoposterior angle. Anepimeron with macroseta anteriorly. Anatergite asetose. *Wings:* Alula well-developed. Costal vein circumambient. Vein R_{2+3} ending in Costal vein, cell r_1 thus open at wing margin. *Legs:* Fore tibia without spine-like tibial processes. Tarsi with pulvilli. Hind tarsus of males with laterally compressed and blade-like empodium.

Abdomen: T2 wider than long. Female terminalia with divided T10, bearing acanthophorite macrotrichia.

Empodiodes greatheadi Oldroyd, 1972

Figs 1, 16

Empodiodes greatheadi Oldroyd, 1972: 635–9 (figs 1 head lateral, 2 head anterior, 4 metathoracic tarsomere 1, 5 prothoracic tarsus); 1974: 166–8 (figs 162 metathoracic tarsomere 1, 163 prothoracic tarsus, 164 head lateral, 165 head anterior); 1980: 361 (catalogue); Londt 1992: 57–59 (figs 1 antenna, 2 prosternum, 3 wing, 4 metathoracic tarsus, 5 empodium, 6 metathoracic pulvilli, 7–9 ♂ terminalia, 10 metathoracic tarsus 5, 11–13 ♀ terminalia).



Figure 1. *Empodiodes greatheadi* Oldroyd, 1972 holotype. Scale bars: in mm. (Photo BMNH).

Material. SOUTH AFRICA: 2♂ Grahamstown [= Grahamstown], Rockhurst [farm 33°10'59"S, 26°19'01"E c. 650m], 13.x.1981, F.W. & S.K. Gess, 81/82/2, AMGS 101476, AMGS 101477 (AMGS); 1♀ Grahamstown, Hilton [farm 33°15'00"S, 26°21'12"E c. 490m], 22.x.1967, C. Jacot-Guillarmod AMGS 101478 (AMGS); ♂ Holotype 'South Africa / C.P. [Cape Province] Alicedale [33°19'S, 26°05'E c. 285m] / 16.xii.71 / D. & A. Greathead' NHMUK010628725 (BMNH); 1♂ 'So. Africa: Cape Prov / 9 km SW Willowmore [c. 33°20'S, 23°27'E 935m] / 30–31.x.1978 3323AD / J Londt & R Miller / open Karoo scrub', NMSA-DIP 81676 (NMSA). *Note:* Holotype not personally handled, but excellent photographs supplied confirm identification.

Distribution, phenology and biology. Entire holotype as in Fig. 1. Known from 5 specimens collected at 4 localities in the Eastern Cape Province of South Africa (Fig. 16). They were collected in October and November (Table 1) in an area located between summer and winter rainfall regions. The only useful label data relating to habitat are the words 'open Karoo scrub' which describes much of the area. No other biological data are available.

Table 1. Phenology of *Empodiodes* species indicating the number of specimens collected per month (abbreviated and starting with July).

Species	J	A	S	O	N	D	J	F	M	A	M	J
<i>E. greatheadi</i>	–	–	–	4	–	1	–	–	–	–	–	–
<i>E. melanoscopaeus</i>	–	–	–	–	4	–	–	–	–	–	–	–
<i>E. namibiensis</i>	–	4	–	36	–	–	–	–	–	–	–	–
<i>E. pusillipes</i> sp. nov.	–	–	1	2	–	–	–	–	–	–	–	–
<i>E. torridus</i> sp. nov.	–	–	1	–	–	–	–	–	–	–	–	–
<i>E. whittingtoni</i>	–	–	–	–	1	–	–	–	–	–	–	–
Total	0	4	2	42	5	1	0	0	0	0	0	0

***Empodiodes melanoscopaeus* Londt, 2012**

Figs 2, 16

Empodiodes melanoscopaeus Londt, 1992: 59–62 (figs 15 head anterior, 15 head lateral, 17 prosternum and prothoracic coxae, 18 wing, 19 metathoracic tarsus, 20–21 metatarsal appendages, 22–24 ♂ terminalia); 2012: 260–3 (figs 1 entire ♂, 2 head lateral, 3 metathoracic tarsus, 4 wing, 5–7 ♂ terminalia, 8 ♀ terminalia); 2012: 263.

Material. SOUTH AFRICA: 1♂ 1♀ 'South Africa: N Cape / 1 km S Carnarvon 1260m / Appie van Heerden Nat. / Reserve 14.xi.2008 / 30°58.83'S, 22°07.39'E / J & A Londt Karoo scrub' NMSA-DIP 81677(NMSA); 1♀ Paratype 'S Africa: Cape #33 / 23 km SE of Middelpos / 32°01'S, 20°25'E 1200m / Date: 28.xi.1990 / Whittington & Londt / Banks of Visrivier' NMSA-DIP 74275 (NMSA); ♂ Holotype 'S Africa: Cape #26 / 18km N of Sutherland / 32°16'S, 20°41'E 1350m / Date: 26.xi.1990 / Londt & Whittington / Renosterrivier area' NMSA-DIP 74274 (NMSA).

Distribution, phenology and biology. Known from three localities in the Northern Cape Province of South Africa (Fig. 16) and collected only in November (Table 1). The rather arid areas concerned experience very cold winters and very hot summers so the species may only be active for a brief period between these two possibly unfavourable seasons. Fig. 2, although not taken at one of the known localities, provides an impression of the environment probably inhabited by this species. Little is known of the biology apart from the fact that those individuals collected were perched on the ground and have been collected sympatrically with *E. whittingtoni*.

***Empodiodes namibiensis* Londt, 2012**

Fig. 16

Empodiodes namibiensis Londt, 2012: 260–263 (figs 1 entire ♂, 2 head lateral, 3 metatarsus, 4 wing, 5–7 ♂ terminalia, 8 ♀ terminalia);

Material. NAMIBIA: ♂ Holotype 'Namibia: Opuwa Dist. / 35km E Epupa: Kunene River / 17°03'31"S, 13°29'32"E / 09–11.x.1999 / Kirk-Spriggs Pape Hau-



Figure 2. A typical landscape in the vicinity of Besemgoedkop (photographed 18 November 2011), showing the general habitat occupied by both *Empodiodes melanoscopaeus* and *E. whittingtoni*.

wanga / Malaise trap shaded woodland' NMSA-DIP 74281 (NMSA); 3♂ 2♀ paratypes same date as holotype NMSA-DIP 74276-80, (NMSA); 19♂ 6♀ paratypes same data as holotype (NMWN); 1♂ 1♀ 'Namibia: Opuwa District / Ekuja village: Kunene River / 17°19'30"S, 13°48'56"E / 11–12.x.1999 / Kirk-Spriggs Pape Hauwanga / 'Malaise traps, riverine forest' (NMWN); 3♂ 1♀ 'Ondorusu Falls / SE 1713Bb [17°23'01"S, 13°54'55"E] / Kaokoland / 23–26 Aug 1973', 'H13834' (NMWN); 3♂ 'Namibia: Khorixas Dist. / SE Sorris Sorris: Ugab River / 20°59'09"S, 14°47'32"E / 05–06.x.1999 / Kirk-Spriggs, Pape & / Hauwanga / Malaise trap sample' (NMWN).

Distribution, phenology and biology. Collected at four localities in northern Namibia (Fig. 16), mostly in the vicinity of the Kunene River, during the months of August and October (Table 1). The habitats have been described as 'shaded woodland' and 'riverine forest'. Much of the material was collected in malaise traps, which is surprising as small, ground-dwelling asilids are not usually collected in significant numbers with such traps. The fact that over 30 specimens were collected in 3 days suggests that population numbers were high and, as only eight were female, it appears that males are more active fliers than females.

***Empodiodes pusillipes* sp. nov.**

<http://zoobank.org/479EBC66-54B2-4E59-A6B2-65056E398E21>

Figs 3, 4, 6–8, 12, 13, 16

Etymology. *L. pusillus* (small) + *pes* (foot). Refers to the relatively poorly developed male metathoracic empodia. Noun in apposition.

Description. Based on all material studied. Entire holotype as illustrated (Fig. 3).

Head: Dark red-brown to black, colour masked by strong gold-silver pruinescence, black and white setose. Antenna dark red-brown to black, scape and pedicel white setose, postpedicel laterally compressed and markedly curved outwards. Relative lengths of segments (scape as 1) Scape 1, pedicel 0.3, postpedicel 3.1, style 0.5 (including terminal seta-like sensory element). Face black, slightly protuberant, strongly silver pruinose. Mynthax white, covering ventral $\frac{3}{4}$ of face. Frons and vertex smoothly rounded (not indented between eye margins) gold-silver pruinose, black setose. Ocellar tubercle only weakly protuberant, weakly setose and lacking strong ocellar macrosetae. Occiput gold-silver pruinose, black (dorsally and along eye margins) and white (ventrally) setose. Palps small, 2-segmented, orange, white setose. Proboscis dark red-brown, straight, white setose.

Thorax: Dark red-brown to black, entirely silver and silver-gold pruinose, black and white setose. Cervical sclerite white setose. Anterior antepronotum with a row of black macrosetae. Mesonotum patterned with silver and gold pruinescence, predominantly black setose, but some white setae present. Lateral macrosetae black (2 notopleurals, 2 supra-alars, 2 postalars). Scutellum dark red-brown to black, with *c.* 12 white (\varnothing has a few black ones) apical macrosetae, disc fine silver pruinose, asetose. Pleura silver and gold pruinose, fine white setose. Anepimeron with 1 white anterodorsal macroseta. Katatergal setae well developed, mixed black and white macrosetose. Anatergites silver pruinose, asetose. Postmetacoxal area membranous. **Legs:** Mainly dark red-brown to black but femora and tibiae brown-orange dorsally. Coxae silver pruinose, mostly white setose (a few black setae may be present). Trochanters white setose, femora, tibiae and tarsi fine white setose with black macrosetae. Claws and pulvilli well developed. Empodia yellow, bristle-like except for metathoracic legs where empodia are moderately well developed, dark red-brown and laterally compressed. **Wings** (Fig. 4): Length (humeral crossvein to tip) \times breadth (maximum): Holotype σ 3.8 \times 1.4 mm, paratype \varnothing 4.2 \times 1.6 mm, paratype σ 3.0 \times 1.1 mm. Veins dark red-brown to black, membrane transparent, entirely microtrichose, cells m_3 and cua closed and stalked.

Abdomen: Dark red-brown to black, entirely fine silver and silver-gold pruinose, black and white setose. Terga $>$ twice as wide as long. Terga and sterna black (medially) and white (laterally) setose, T1 with *c.* 4 black discal macrosetae.

Male terminalia (Figs 6–8): Rotated through *c.* 90° anticlockwise. Epandrium *c.* 3 \times wider than long in dorsal view; posterior margin clearly indented medially. Proctiger slightly longer than epandrium in lateral view. Hypandrium subtriangular, twice as broad as long, distinctly pointed posteromedially. Gonocoxites relatively large, higher than long in lateral view, with broad dorsal and finger-like median lobes best seen in



Figure 3. *Empodiodes pusillipes* sp. nov. entire holotype ♂ (Photo Pillay).

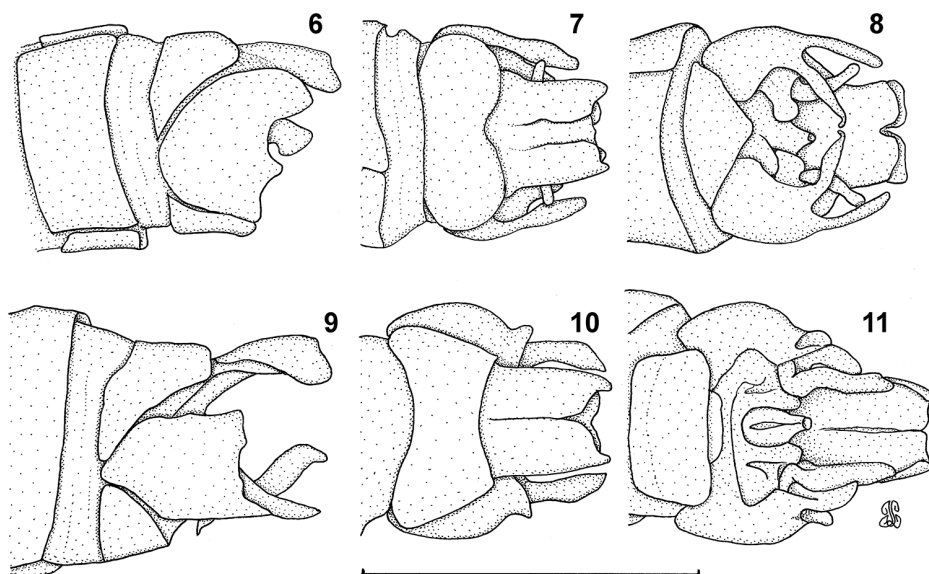


4



5

Figures 4, 5. *Empodiodes* wings: **4** *E. pusillipes* sp. nov. **5** *E. torridus* sp. nov.



Figures 6–11. *Empodiodes* ♂ terminalia: 6–8 *E. pusillipes* sp. nov. 6 lateral 7 dorsal 8 ventral, 9–11 *E. torridus* sp. nov. 9 lateral 10 dorsal 11 ventral. Scale bar: 1 mm.

ventral view. Gonostyli well developed, jutting out laterally between proctiger and gonocoxite. Distal region of aedeagus conical with terminal opening.

Female terminalia (not dissected): Ovipositor tubular (i.e. not laterally or dorsally compressed), subgenital plate with shallow longitudinal midventral keel. T10 bilobed (= acanthophorites), each lobe appearing to bear only 4 stout macrotrichia.

Type Material. Holotype. South Africa (Western Cape Province): 1♂ holotype ‘Sth Africa: W Cape / Vrolijkheid Nature Res / 33°55′01″S, 19°52′43″E / J&A Londt 9–10.x.2013 / 185m *Acacia* rocky / vynbos with succulents’ NMSA-DIP 81678 (NMSA).

Paratypes: 1♀ paratype – data identical to holotype NMSA-DIP 81679 (NMSA); 1♂ paratype ‘Sth Africa: W Cape / 2 km S of Papendorp / 31°43′01″S, 18°12′22″E / J&A Londt 10.ix.2012 / 15m Vegetated dunes’ NMSA-DIP 81680 (NMSA).

Distribution, phenology and biology. Known from two localities in the Western Cape Province of South Africa (Fig. 16) and collected in September and October (Table 1). Localities clearly fall within a winter rainfall region. Apart from being collected in sandy localities dominated by vynbos, nothing is known of the biology. Figs 12, 13 give an impression of the environments where the species has been collected.

Empodiodes torridus sp. nov.

<http://zoobank.org/44E36783-2435-4A19-AFFB-993AB98312D2>

Figs 5, 9–11, 14–16

Etymology. *L. torridus* – dry, parched, hot, scorched – a name referring to the fairly dry and semi-arid environment supporting the species.



Figure 12. *Empodiodes pusillipes* sp. nov. habitats at Vrolijkheid Nature Reserve (photographed 11 October 2013).



Figure 13. *Empodiodes pusillipes* sp. nov. habitats at 2 km S of Papendorp (photographed 10 September 2012), where the species was collected.

Description. Based on holotype. Entire holotype (Fig. 14) photographed before the removal of its right wing and terminalia. The specimen is attached to a card preventing examination of parts of its left side.

Head: Dark red-brown to black, colour masked by strong gold-silver pruinescence, yellow and white setose. Antenna dark red-brown to black, scape and pedicel white setose, postpedicel laterally compressed and markedly curved outwards. Relative lengths of segments (scape as 1) Scape 1, pedicel 0.5, postpedicel 3.2, style 0.4 (including terminal seta-like sensory element). Face black, slightly protuberant, strongly gold-silver pruinose. Mystax white, covering almost entire face. Frons and vertex smoothly rounded (not indented between eye margins) silver-gold pruinose, pale yellow and white setose. Ocellar tubercle only weakly protuberant, weakly setose and lacking strong ocellar macrosetae. Occiput silver and gold pruinose, yellow (dorsally) and white (ventrally and along eye margins) setose. Palps small, 2-segmented, orange, pale yellow setose. Proboscis brown, straight, weakly white setose.

Thorax: Dark red-brown and orange, entirely silver and silver-gold pruinose, yellow and white setose. Cervical sclerite white setose. Anterior anteprepronotum with a row of pale yellow macrosetae. Mesonotum patterned with silver and gold longitudinal pruinose stripes, predominantly yellow setose, but some white setae present. Lateral macrosetae yellow (2 notopleurals, 1–2 supra-alars, 2 postalars). Scutellum dark red-brown, with *c.* 12 white apical macrosetae, disc fine silver pruinose, asetose. Pleura silver and gold pruinose, fine white setose. Anepimeron with 2 weak white anterodorsal macrosetae. Katatergal setae moderately well developed, pale yellow macrosetose. Anatergites silver pruinose, asetose. Postmetacoxal area probably membranous (hidden from view). *Legs:* Mainly light brown to yellow, but dorsal parts of femora and entire tarsi dark red-brown. Coxae silver pruinose, white setose. Trochanters white setose, femora, tibiae and tarsi white setose. Claws and pulvilli well developed. Empodia yellow, bristle-like except for metathoracic legs where empodia are moderately well developed, brown and laterally compressed. *Wings* (Fig. 5): Length (humeral crossvein to tip) \times breadth (maximum): Holotype ♂ 3.3×1.4 mm. Veins dark red-brown to black, membrane transparent, entirely microtrichose, cells m_3 and cua closed and stalked.

Abdomen: Dark red-brown and orange, entirely fine silver and silver-gold pruinose, pale yellow and white setose. Terga $>$ twice as wide as long. Terga and sterna dark red-brown with broad orange distal margins, fine white setose, T1 with *c.* 5 white discal macrosetae.

Male terminalia (Figs 9–11): Unrotated. Epandrium subrectangular in dorsal view, twice as broad as long, with posterior margin slightly indented medially. Proctiger of similar length to epandrium in lateral view. Hypandrium subrectangular, twice as broad as long with an almost straight posterior margin. Gonocoxites relatively large, with complex structure involving twisted ventro-distal projections. Gonostyli well developed, jutting out beyond level attained by gonocoxal projections. Distal region of aedeagus conical with terminal opening.

Female: Unknown.



Figure 14. *Empodiodes torridus* sp. nov. entire holotype ♂ (Photo Muller).

Type Material. Holotype. South Africa (Northern Cape Province): 1♂ holotype ‘S. Africa, C.P. / Van Wyk’s Fontein / Colesberg / 3038S, 2523E’, ‘22 Sept. 1983 / Entomology Dept’, BMSA(D) 01390.

Distribution, phenology and biology. Known only from the single specimen listed above, collected in September (Table 1) in a far eastern corner of the Northern Cape Province of South Africa (Fig. 16). The locality is situated in the fairly arid Nama-Karoo biome (Van Wyk and Smith 2001) which lies in a summer rainfall region. While the type locality has not been photographed, Fig. 15 illustrates the kind of environment in which this species was probably collected. Nothing is known of the biology.

Empodiodes whittingtoni Londt, 1992

Figs 2, 15

Empodiodes whittingtoni Londt, 1992: 62–63 (figs 25 antenna, 26 prosternum, 27 metathoracic tarsal appendages, 28 empodium, 29–31 ♂ terminalia);

Material. SOUTH AFRICA: 1♂ holotype ‘S Africa: Cape #33 / 23 km SE of Middelpos / 32°01'S, 20°25'E 1200m / Date: 28.xi.1990 / Whittington & Londt / Banks of Visrivier' NMSA-DIP 74273 (NMSA).



Figure 15. A typical Karoo landscape at Doornfontein Nature Reserve (photographed 21 March 2006), representative of the environment in which *Empodiodes torridus* sp. nov. has been collected.

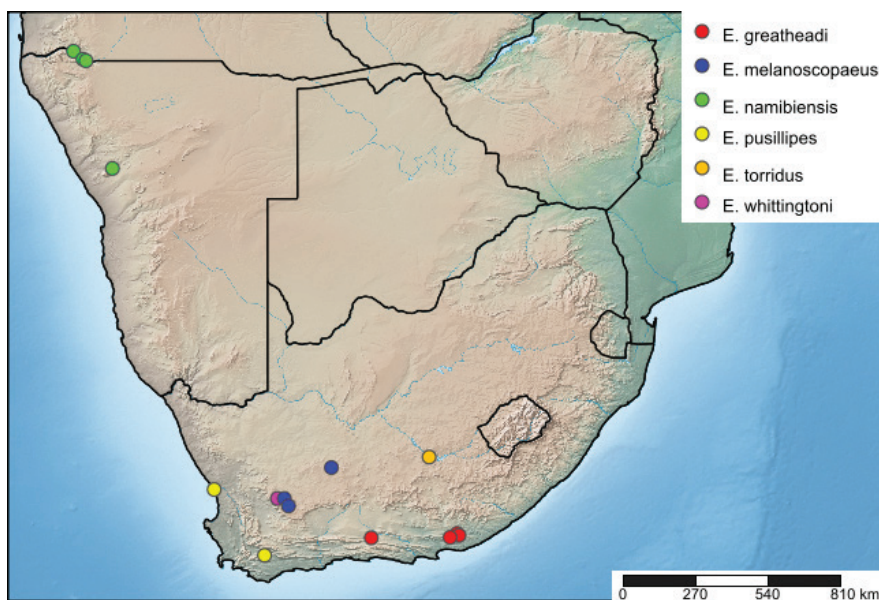


Figure 16. The distribution of *Empodiodes* species: *E. greatheadii* Oldroyd, 1972 (●), *E. melanoscopaeus* Londt, 1992 (○), *E. namibiensis* Londt, 2012 (■), *E. pusillipes* sp. nov. (□), *E. torridus* sp. nov. (▲), *E. whittingtoni* Londt, 1992 (◆) (Map Zamisa).

Distribution, phenology and biology. Recorded only from the type locality in the Northern Cape Province of South Africa (Fig. 16) and collected sympatrically with *E. melanoscopaeus* in November (Table 1), resting on a rock. While the type locality was not photographed, Fig. 2 provides an impression of the habitat in the vicinity of the type locality.

Discussion

Key to species of *Empodiodes*

- 1 Smaller species, wing <6 mm in length; laterally compressed and enlarged empodia confined to metathoracic legs of males.....2
- Larger species, wing >6 mm in length; laterally compressed and enlarged empodia present on all legs of males5
- 2 Mystax predominantly, if not entirely, black (southern parts of Northern Cape Province of South Africa) *E. melanoscopaeus* Londt, 1992
- Mystax predominantly, if not entirely, white3
- 3 Mesonotal macrosetae predominantly, if not entirely, black; abdominal terga entirely dark red-brown to black (Western Cape Province of South Africa) ...
..... *E. pusillipes* sp. nov.
- Mesonotal macrosetae yellow or white; abdominal terga entirely or partly yellow.....4
- 4 Mesonotal macrosetae predominantly, if not entirely, white; abdominal terga extensively, if not entirely, yellow (northern Namibia: primarily Kunene Region) *E. namibiensis* Londt, 2012
- Mesonotal macrosetae predominantly, if not entirely, yellow; abdominal terga proximally dark red-brown, distally yellow (eastern Northern Cape Province of South Africa) *E. torridus* sp. nov.
- 5 Mystax and other major macrosetal groups black (Eastern Cape Province of South Africa) *E. greatheadi* Oldroyd, 1972
- Mystax and other major macrosetal groups white (southern Parts of Northern Cape Province of South Africa) *E. whittingtoni* Londt, 1992

Distribution, phenology and biology

The known distribution of the genus is shown in Fig. 16. Species are bound to be far more widely distributed as the rather arid and fairly uniform nature of their preferred habitat has not attracted much sampling activity. The fact that *E. namibiensis* has been collected in significant numbers in malaise traps testifies to the probability that these tiny flies are far more abundant than currently available data suggest. Species have only been collected from August through to November (Table 1) which prob-

ably suggests that this period, between very cold, and sometimes wet, and very hot and dry conditions, is most conducive for adult activity. It also appears that species are all ground dwellers, probably preferring sandy substrates, i.e. ecological category 1c (Londt 1994b). The fact that the laterally compressed empodia, so characteristic of the genus, is a feature confined to males suggests that these serve a purpose during courtship behaviour.

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